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RELATIONSHIPS OF TRACYINA AND RIGIOPAPPUS (COMPOSITAE)

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The relationships between *Tracyina* Blake and *Rigiopappus* Gray have been discussed briefly by various authors (e.g., Blake, 1937; Raven and Kyhos, 1961) but not until recently have the morphological characters of these monotypic genera been discussed in any detail. Van Horn (1973) and Robinson and Brettell (1973) suggest that despite their traditional placement in different tribes, these two genera are similar to each other in a number of respects, also resemble *Chaetopappa* and *Pentachaeta* (both Astereae), and properly belong in Astereae. In this paper we present additional evidence, from chromosomal, biochemical, and hybridization studies, that indicates unequivocally that *Tracyina* and *Rigiopappus* are very closely related to each other.

Methods and Materials

In 1960 the first author collected achenes of *Tracyina rostrata* Blake from the type locality (Alder Point, Humboldt County, California, *Ornduff 6185,* UC), one of two sites at which this rare species is known to occur (Keck, 1959). Plants of this annual species have been grown at the University of California Botanical Garden on several occasions since the initial collection; these cultivated plants were used in this study. *Rigiopappus leptocladus* Gray is widespread in the western United States, and three collections of this species were used in this study (Mount Hamilton, Santa Clara County, California, *Ornduff 6045;* Lake Berryessa, Lake County, California, *Ornduff 6108;* Scott Mountain, Trinity County, California, *Ornduff 6273,* all UC).

Tracyina has a chromosome number of $2n = 9_{II}$, as does *Rigiopappus* (Raven and Kyhos, 1961). Plants of both species and their artificial hybrids were examined for their flavonoid constituents, using living plants or dried material that was processed according to a method outlined in detail elsewhere (Bohm et al., 1974).

Intergeneric Hybridization

Because of their small size, it is very difficult to emasculate the hermaphroditic florets of either species, but it was possible to hybridize *Rigiopappus* and *Tracyina* by applying pollen of the latter to the pistillate marginal florets of the former. Two hybrid individuals were obtained from a cross between these genera *(Ornduff 6273 × 6185)*. These plants were vigorous, attaining a stature greater than that of either parent, and were intermediate between the parents in foliar and pappus characters. Examination of 100 pollen grains stained with aniline blue-lactophenol indicated viabilities of 99 percent for the parents and 31 and 36 percent, respectively, for the two hybrids. Study of hybrid meiosis by D. W. Kyhos indicated at diakinesis seven bivalents plus a ring of four chromosomes. This configuration suggests a very high degree of chromosomal homology between these two taxa. Despite their moderate degree of pollen viability the hybrids produced no mature achenes.

Flavonoid Studies

Kaempferol, quercetin, and isorhamnetin were identified in *Rigiopappus,* each occurring in the form of 3-0-glucoside and 3-0-rutinoside. The kaempferol and quercetin glycosides are shared with *Tracyina,* but this genus lacks isorhamnetin glycosides. The intergeneric hybrids produced the flavonoids of the parents.

The simplest of the possible biosynthetic relationships among the three flavonoid constituents of these genera is a simple and linear one. Kaempferol, a compound shared by both genera, may produce quercetin by addition of a hydroxyl group. Isorhamnetin may be produced by means of an O-methylation of quercetin. This last biochemical step is apparently carried out by *Rigiopappus* and the intergeneric hybrids, but it does not occur in *Tracyina.*

Discussion

Rigiopappus, Tracyina, and *Pentachaeta* all have a similar habit, termed the "herba impia" habit by Blake (1937; see also Van Horn, 1973). *Tracyina* and *Pentachaeta* are both members of Astereae, but the tribal affinities of *Rigiopappus* have been a matter of dispute. Chiefly because of its marginal receptacular bracts that are internal to the ray florets, *Rigiopappus* has traditionally been assigned to Helenieae (e.g. Hoffmann, 1889; Cronquist, 1955; Keck, 1959). More recently, Robinson and Brettell (1973) have stated that the stamens of *Rigiopappus* are "Asterean in all respects". Indeed, marginal receptacular bracts are

known to occur in some species of typical genera of Astereae such as *Haplopappus, Petradoria, Bigelowia, Chrysothamnus* (Loran Anderson, pers. comm.), and *Solidago* (Morton, 1968), and in *Tracyina* there are occasional receptacular bracts interior to the ray florets. One of the most striking differences between the two genera is in the nature of the pappus, consisting of 24–40 capillary bristles in *Tracyina* and 3–5 awnlike scales in *Rigiopappus*. The 10–15 pappus bristles of the intergeneric hybrid are intermediate in width.

Chromosomal and biochemical similarities between the genera argue for a close relationship. Intergeneric hybrids are vigorous, produce some viable pollen, and show a high degree of chromosomal homology. Both genera have four of six flavonoid compounds in common. The flavonoid produced by one genus but not the other may require only a simple O-methylation of a compound occurring in both species, a chemical transformation that could be controlled by a single gene (Harborne, 1967). This evidence from diverse sources leads us to the conclusion that *Tracyina* and *Rigiopappus* are very close relatives that should be placed side by side in Astereae. One could, indeed, use this evidence to argue for the congeneric status of these two taxa. However, the magnitude of the differences between them in some pappus, achene, and capitular characters is sufficiently great that we believe both taxa should be maintained as distinct monotypic genera.

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